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Geographic variability in *Calligrapha verrucosa* (Suffrian 1858),
a willow-feeding leaf beetle from western North America
(Coleoptera: Chrysomelidae)

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Abstract. A diagnosis is provided to separate *Calligrapha verrucosa* (Suffrian) from similar species. Geographic variability is described and illustrated for various populations of *C. verrucosa*. A map is provided to indicate the distribution of this species.

Introduction

The genus *Calligrapha* was originally described by Chevrolat in 1836. Later, Chevrolat (1843) designated the South American species *Chrysomela polyspila* Germar to be the type species. As currently constituted, the genus is comprised of the four subgenera *Calligrapha* Chevrolat, *Bidensomela* Monrós, *Calligramma* Monrós, and *Graphicallo* Monrós. Whereas some of these subgenera include regularly striped species, devoid of isolated elytral spots, the subgenus *Calligrapha* [including *C. polyspila* and *C. verrucosa* (Suffrian)] can generally be recognized by the numerous isolated speckles. The only other chrysomelid genus in the United States and Canada that includes species with similarly speckled elytra is *Zygogramma* Chevrolat, which is easily recognizable due to the connate tarsal claws, in contrast to the diverging claws of *Calligrapha*. Beetles in the subgenus *Calligrapha* are rather large, typically 7-10 mm long. As their name (Greek for beautiful writing) suggests, the insects, with their winding stripes and speckles, are very showy.

These beetles are still in need of considerable investigation, taxonomic and otherwise. In spite of the fact that Brown (1945) did a rather detailed investigation of the taxonomy and host plants of the species occurring in eastern Canada, and the fact that other important studies dealing with chromosomal structure, biogeography, speciation, and species diagnosis have subsequently been published by workers such as Robertson (1966), Gómez-Zurita (2005), and Gómez-Zurita et al. (2004, 2006), species identification is difficult due to the similarity among species and the variability of markings within species. It is difficult, or perhaps impossible, to find two specimens with exactly the same markings. The situation is complicated further by parthenogenesis in some species. As should be expected, each parthenogenetic lineage, unable to interbreed with other populations, is a little different. Although some asexual lineages probably should be recognized as distinct species, other named forms might better be regarded as mere strains, not nomenclaturally distinct from close relatives. Aedeagal characters show promise for separating some species, but they are poorly studied, and they are lacking in parthenogenetic species.

A number of years ago, we encountered several pale specimens of *Calligrapha* that did not match the description of any known species. Although they were similar to *C. verrucosa*, they differed from material available for comparison in both color pattern and details of punctuation. Initially, we thought that they belonged to an undescribed species. Subsequent study of numerous specimens from many localities demonstrates that they are only variants of *C. verrucosa*. We herein describe and illustrate this variability. We prefer not to name subspecies. Although there are a few instances of striking differences in appear-

ance between nearby populations, the variability is often gradual, and intermediate morphological characters occur in intermediate areas.

Materials and Methods

This investigation is not a full-blown taxonomic revision, and no attempt was made to examine all available specimens. Even so, sufficient material was examined to document and characterize the intraspecific variability of *C. verrucosa*. Specimens were borrowed from the following curators and collections (acronyms following the entries are referred to in the Material Examined section and generally follow acronyms in Arnett et al. 1993): Michael F. Whiting, Brigham Young University, Provo, Utah (BYUC); Norman Penny, California Academy of Sciences, San Francisco, California (CASC); Charles L. Bellamy, California Department of Food and Agriculture, Sacramento, California (CDAE); William H. Clark, Albertson College of Idaho, Caldwell, Idaho (CIDA); Boris C. Kondratieff, Colorado State University, Fort Collins, Colorado (CSUC); Edward G. Riley, Edward G. Riley Collection, College Station, Texas (EGRC); Cheryl B. Barr, University of California, Berkeley, California (EMEC); Wilford J. Hanson, Utah State University, Logan, Utah (EMUS); Scott R. Shaw, University of Wyoming, Laramie, Wyoming (ESUW); Michael C. Thomas, Florida State Collection of Arthropods, Gainesville, Florida (FSCA); Paul P. Tinerella, Illinois Natural History Survey, Champaign, Illinois (INHS); Karla Schneider, Martin-Luther-Universität, Halle, Germany (MLUH); Michael A. Ivie, Montana State University, Bozeman, Montana (MTEC); Edward G. Riley, Texas A&M University, College Station, Texas (TAMU); Lynn S. Kimsey, University of California, Davis, California (UCDC); Brett C. Ratcliffe, University of Nebraska, Lincoln, Nebraska (UNSM); Frank W. Merickel, University of Idaho, Moscow, Idaho (WFBM).

The references cited in the following synonymy section are not exhaustive. They are limited to the original description and a few of the more important subsequent references.

Calligrapha verrucosa (Suffrian)

Chrysomela verrucosa Suffrian 1858: 266.

Calligrapha verrucosa (Suffrian): Schaeffer 1934: 477; Brown 1945: 123; Robertson 1966: 715; Hatch 1971: 184; Wilcox 1972: 6; Gómez-Zurita 2005: 95.

Diagnosis. Among the United States and Canadian species of the subgenus *Calligrapha* (this subgenus being characterized by an elytral pattern that includes numerous isolated spots), *C. verrucosa* differs from most others in having the pronotum bicolored, or unusually entirely pale, but not entirely dark. Beyond this, the elytra of *C. verrucosa* have a sutural or subsutural stripe that is distinctly paler than the elytral speckles. In the palest specimens, this stripe is essentially absent, being as light as the pale background. In most other species, whether with or without bicolored pronota, the sutural or subsutural stripe is black, often with metallic luster. Occasional specimens of *C. verrucosa* are difficult to distinguish from *C. multipunctata* (Say), a sympatric species that feeds on the same hosts. The diagnostic characters mentioned above are usually adequate to distinguish these two species. In addition to these characters, the body of *C. verrucosa* is usually more elongate than that of *C. multipunctata*. The aedeagi of the two species are quite different (Fig. 1a, 1b).

Variability. *Calligrapha verrucosa* is quite variable, particularly with regards to the number, appearance, and size of elytral spots, as well as the ventral coloration. Although no two specimens are exactly alike, this variability is generally not noteworthy within a population, but it becomes obvious as specimens are observed from various localities.

The dark maculations on the elytra of specimens from some areas are much less extensive than those from other areas. In extreme cases, populations have lost nearly all elytral spots. In contrasting populations from some other areas, the maculae are large, partially coalescent, and covering about half of the elytral surface.

In general, northern populations are darker than those in the South, and this change is gradual, with no abrupt delineation of morphological groups (Fig. 2). However, some southern populations, such as

those in Nevada (Fig. 2 k-n), are actually darker than the lightest forms found at the Bruneau Sand Dunes in southern Idaho (Fig. 2 p-r). The darkest specimens are found in Alaska, at the northernmost extent of the beetles' range (Fig. 2d), with intermediates usually found at intervening latitudes. There is variability within populations as well, but on a much smaller scale than differences among populations.

In some populations, most notably in Nebraska, each dark spot is elevated above the surrounding elytron (Fig. 3). This swelling of elytral spots is quite different from specimens we have examined from other areas, where there is little variation and little inflation of the maculae.

Coloration of the sternum is also variable. The original description of *C. verrucosa* indicates that the thoracic sternum of type material is reddish in color. However, only some populations, including most of those in Montana, Washington, Wyoming, southern Idaho, and Nebraska, have that appearance (Fig. 4b). Populations in Alaska, Canada, Oregon, northern Idaho, California, and Nevada all have black thoracic sterna, fading into red posteriorly on the abdominal ventrites (Fig. 4a). This ventral coloration tends to be less variable within populations than is the elytral coloration.

Most of the apparent geographic variability can be summed up in the three characters discussed above. Aedeagi of specimens from Alaska, the Northwest Territories, Saskatchewan, Montana, Idaho, Nevada, and Nebraska were examined for variation, but no noteworthy differences were detected.

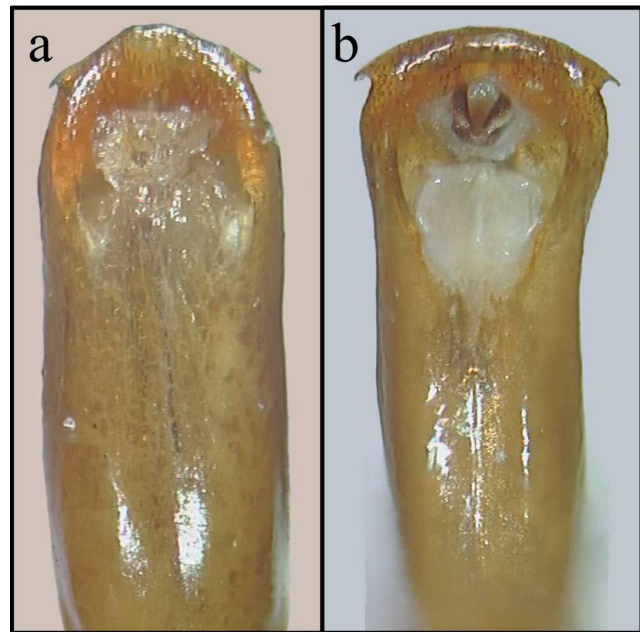


Figure 1. Dorsal views of the aedeagi. **a)** *Calligrapha verrucosa*. **b)** *Calligrapha multipunctata*.

Material examined. Following each entry in this section, the number of specimens is indicated in parentheses, followed by an acronym for the collection in which they are deposited. For an interpretation of the acronyms, see the Materials and Methods section above.

CANADA. ALBERTA: Carbon, C. Garrett (2, CASC); Coolspur, 16-IX-1929, H. Richmond (1, CASC); Drayton Valley, 22-IX-1968, J. H. Frank (4, FSCA); Ft. Fitzgerald, 13-IX-1932, O. Bryant (11, CASC); High River, 12-VI-1925, O. Bryant (1, CASC); McLeod, 28-VIII-1924, F. S. Carr (3, INHS); Medicine Hat, 12-V-1923, F. S. Carr (4, UCDC); Medicine Hat, 22-IV-1925, F. S. Carr (1, INHS); Medicine Hat, 22-IV-1923, F. S. Carr (4, INHS); Medicine Hat, 6-VI-1932, O. Bryant (3, CASC); Oldman River, Hwy. 22, north of Lundbreck, 28-V-1993, R. W. Baumann & L. J. Liu (1, BYUC); Willow Creek, Hwy. 527, southwest of Stavely, 23-V-1993, R. W. Baumann & L. J. Liu (36, BYUC); Willow Creek, Hwy. 527, southwest of Stavely, 23-V-1993, C. E. Campora (1, BYUC). **BRITISH COLUMBIA:** Fernie, 18-VI-1934, H. B. Leech (3, CASC); Fernie, 26-VI-1934, H. Leech (28, CASC; 2, CDAE); Fernie, 19-VII-1934, H. B. Leech (1, CASC); Fernie, 3-VIII-1934, H. B. Leech (2, CASC); Ft. St. John, Peace River, 3-VII-1930, R. Graham (3, CASC); Quesne, 22-VII-1931, J. R. Howell (7, CASC); Quesne, 16-VIII-1932, R. Hopping (9, CASC); 4 mi. N Wardner, 2-VI-1975, Wharton (1, TAMU). **MANITOBA:** Berens Island, Lake Wpg, 9-VII-1918, J. N. Gowanlock, *Salix* sp. (1, INHS). **NORTHWEST TERRITORIES:** Ft. Resolution, 19-IX-1931, O. Bryant (1, CASC); Ft. Simpson, 16-VIII-1929, O. Bryant, willow (40, CASC); Ft. Wrigley, 18-VIII-1929, O. Bryant (1, CASC); Ft. Wrigley, 5-IX-1932, O. Bryant (1, CASC); Good Hope, 23-VIII-1929, O. Bryant (75, CASC); Norman, 13-VII-1930, O. Bryant (30, CASC); Norman, 1-IX-1932, O. Bryant (63, CASC); Simpson, 16-VIII-1929, O. Bryant (9, CASC); Simpson, 1-IX-1932, O. Bryant (2, CASC; 2, CDAE). **SASKATCHEWAN:** Battle River, 26-VIII-1940, A. R. Brooks, willow (2, UCDC); 15 km W Langham, 16-VII-1988, D. W. Webb (1, INHS); Pennant, 13-VII-1935, R. Graham (7, CASC); Pennant, 14-VII-1935, R. Graham (2, CASC); Pennant, 1-VIII-1935, R. Graham (1, CASC); Saskatoon, 17-VIII-1940, A. R. Brooks, willow (2, UCDC);

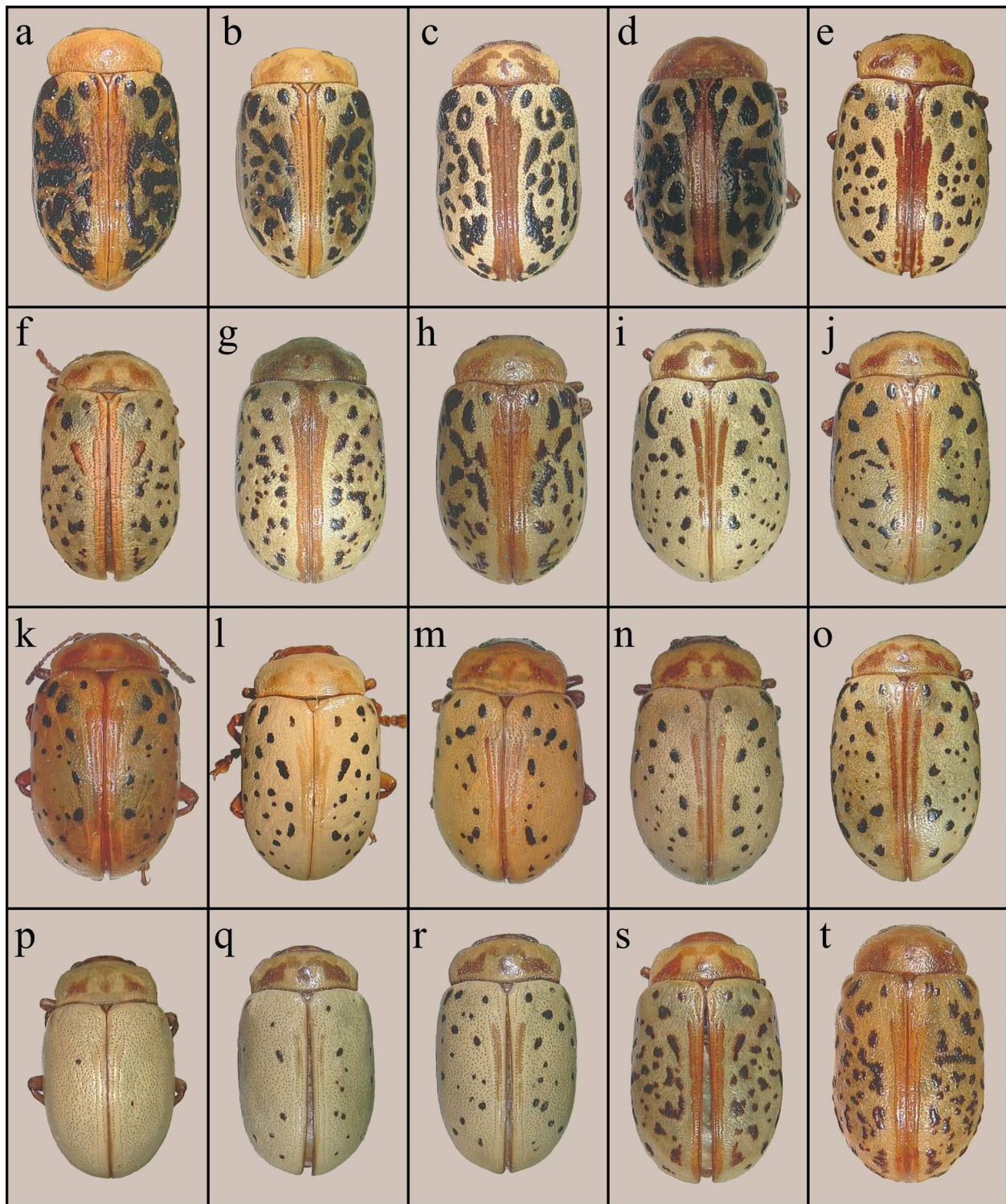


Figure 2. Dorsal habitus views showing variation among populations of *C. verrucosa*. **a-b)** Northwest Territories. **c)** British Columbia. **d)** Alaska. **e)** Washington. **f-h)** Montana. **i-j)** California. **k-n)** Nevada. **o-r)** Idaho. **s)** Wyoming. **t)** Nebraska.

Swift Current, 25-VIII-1939, A. R. Brooks, *Salix* (2, CDAE). **YUKON TERRITORY:** Dawson, 16-VI-1928, A. T. McClay (1, UCDC); [no specific locality] (3, INHS).

USA. ALASKA: Circle, 21-VI-1928, A. T. McClay (10, UCDC); Eagle, 18-VI-1928, A. T. McClay (2, UCDC); Fairbanks, VII-1955, Barisich (1, EMUS); Fairbanks North Star Co., 10 km W Fairbanks, 10-V-1983, M. C. Whitmore, *Salix alaxensis* (25, EMEC); 9 mi. S Fairbanks, Bonanza Creek, 28-V-1982, S. D. Farley (1, CIDA); 20 km SW Fairbanks, Bonanza Creek Experimental Forest, 3-VIII-1982, M. C. Whitmore, willow (2, EMEC); 30 km SW Fairbanks, Bonanza Creek Experimental Forest, 18-V-1983, M. C. Whitmore, *Salix* sp. (7, EMEC); 30 km SW Fairbanks, Bonanza Creek Experimental Forest, 18-V-1983, M. C. Whitmore, *Salix interior* (2, EMEC); Ft. Yukon, 23-VI-1928, A. T. McClay (13, UCDC); Ft. Yukon, 23-VI-1926, R. E. Barrett (1, CASC); Ft. Yukon, 23-VI-1928, R. E. Barrett (3, CASC); Rampart, 17-VII-1916 (1, CASC); Yukon Koyukuk Co., Beaver, 24-VI-1928, A. T. McClay (1, UCDC). **CALIFOR-**



Figure 3. Portion of elytra, showing elevated maculae on a specimen from Nebraska.

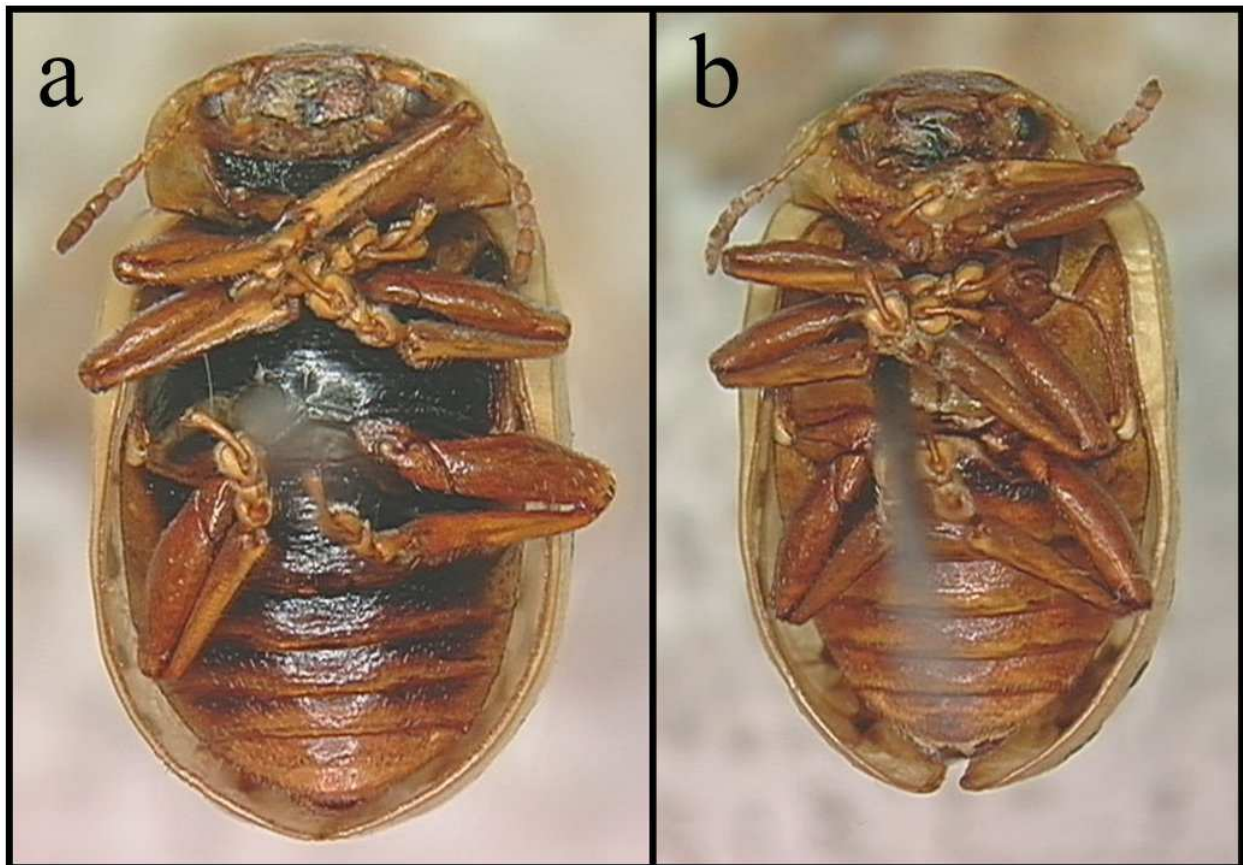


Figure 4. Ventral view of beetles showing coloration of thoracic sternum. **a)** Nevada specimen (dark form). **b)** Montana specimen (light form).

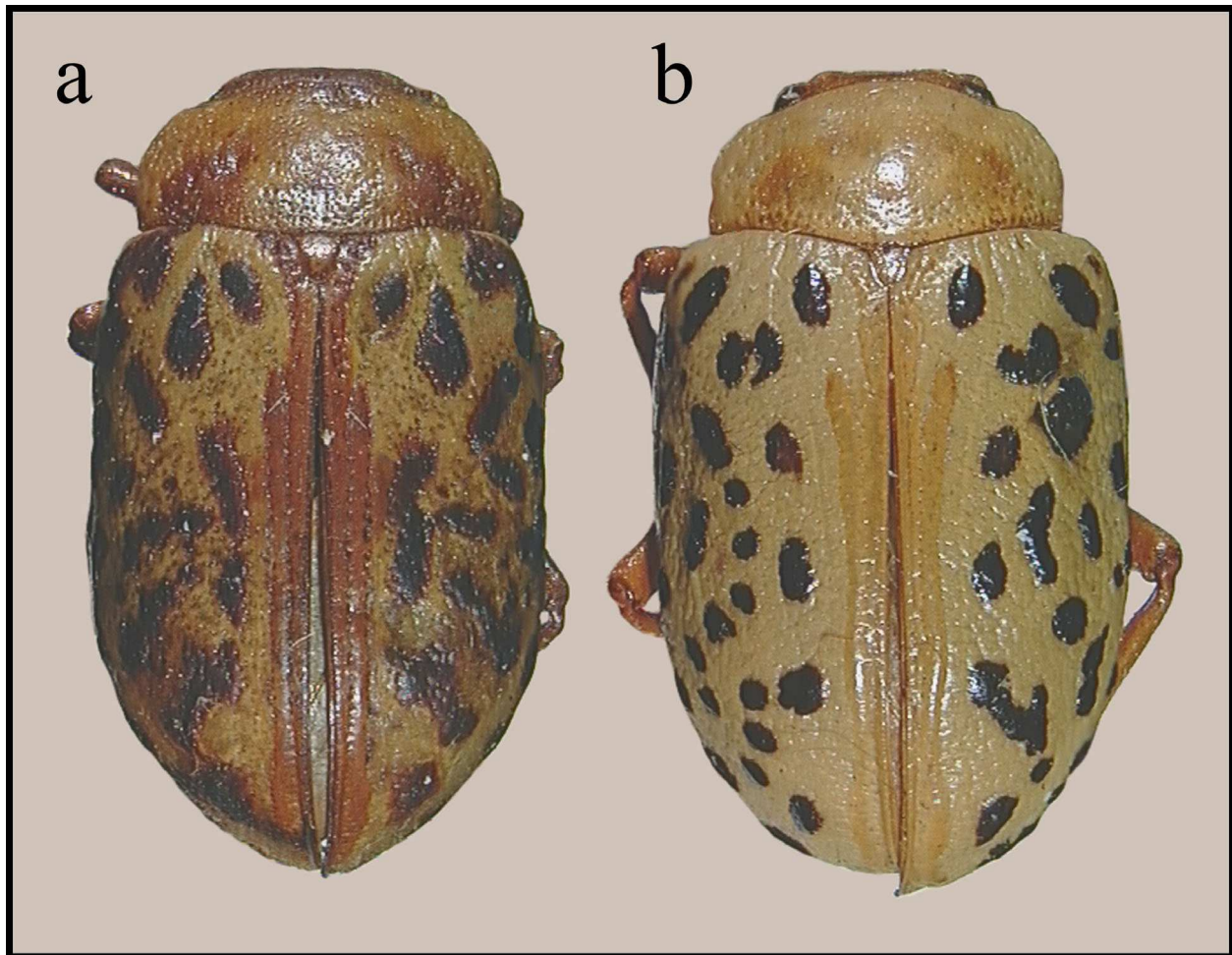


Figure 5. Dorsal view of two specimens identified as *C. verrucosa* in the Suffrian collection at the Martin-Luther-Universität in Halle, Germany. **a)** Specimen 31733 from “Illionis” [sic]. **b)** Specimen 27673 from “Nordamerika.”

NIA: Lassen Co.: 3.5 mi. NW Doyle, elev. 4278 ft., 15-V-1994, J. D. McCarty, willow (5, EMEC); Hallelujah Junction, 11-VII-1961, P. M. Marsh (1, UCDC); Hallelujah Junction, 28-VI-1962, R. J. Gill (8, UCDC); Hallelujah Junction, 28-VI-1962, M. E. Irwin (1, UCDC); Hallelujah Junction, 28-VI-1962, E. J. Montgomery (1, UCDC); Hallelujah Junction, 28-VII-1962, G. W. Frankie (9, EMEC); Hallelujah Junction, 2-VII-1964, E. A. Kane (1, CDAE); Hallelujah Junction, 2-VII-1964, W. K. Thrailkill (1, WFBM); Hallelujah Junction, 28-V-1966, C. R. Kovacic (1, UCDC); Hallelujah Junction, 29-V-1966, C. R. Kovacic (5, UCDC); Hallelujah Junction, 30-V-1966, C. R. Kovacic (7, UCDC); Hallelujah Junction, 29-VI-1966, P. B. Schultz (4, UCDC); Hallelujah Junction, 2-VII-1968, R. M. Bohart (1, UCDC); Hallelujah Junction, 3-VII-1968, C. J. Horning (1, UCDC); Hallelujah Junction, 4-VII-1968, K. F. Doyle (1, FSCA); Hallelujah Junction, 13-VII-1968, R. R. Pinger (8, CDAE); Hallelujah Junction, 9-IX-1968, R. R. Pinger, *Salix* (1, CDAE); Hallelujah Junction, 14-VII-1969, D. E. Foster, on willow (4, WFBM); Hallelujah Junction, 15-VIII-1969, K. S. Hagen (20, EMEC); Hallelujah Junction, 15-IX-1969, R. F. Denno & E. E. Grissell (10, UCDC); Hallelujah Junction, 30-VI-1970, D. S. Chandler (12, UCDC); Hallelujah Junction, 30-VI-1970, E. C. Sickels (3, UCDC); Hallelujah Junction, 30-VI-1970, B. V. Villegas (1, EGRC); Hallelujah Junction, 11-VII-1970, S. R. Sims (6, UCDC); Hallelujah Junction, 10-IX-1971, F. G. Andrews (135, CDAE); Hallelujah Junction, 10-IX-1971, E. A. Kane (24, CDAE); Hallelujah Junction, 28-VI-1972, S. K. Ault (3, UCDC); Hallelujah Junction, 28-VI-1972, R. A. Belmont (3, UCDC); Hallelujah Junction, 28-VI-1972, S. F. Casey (3, UCDC); Hallelujah Junction, 13-VII-1972, S. K. Ault (1, UCDC); Hallelujah Junction, 17-VII-1973, B. Villegas (14, UCDC); Hallelujah Junction, 1-VII-1974, N. J. Smith (1, UCDC); Hallelujah Junction, 29-VI-1976, R. D. Montgomery (4, UCDC); Hallelujah Junction, 29-VI-1976, R. F. Otondo (3, UCDC); Hallelujah

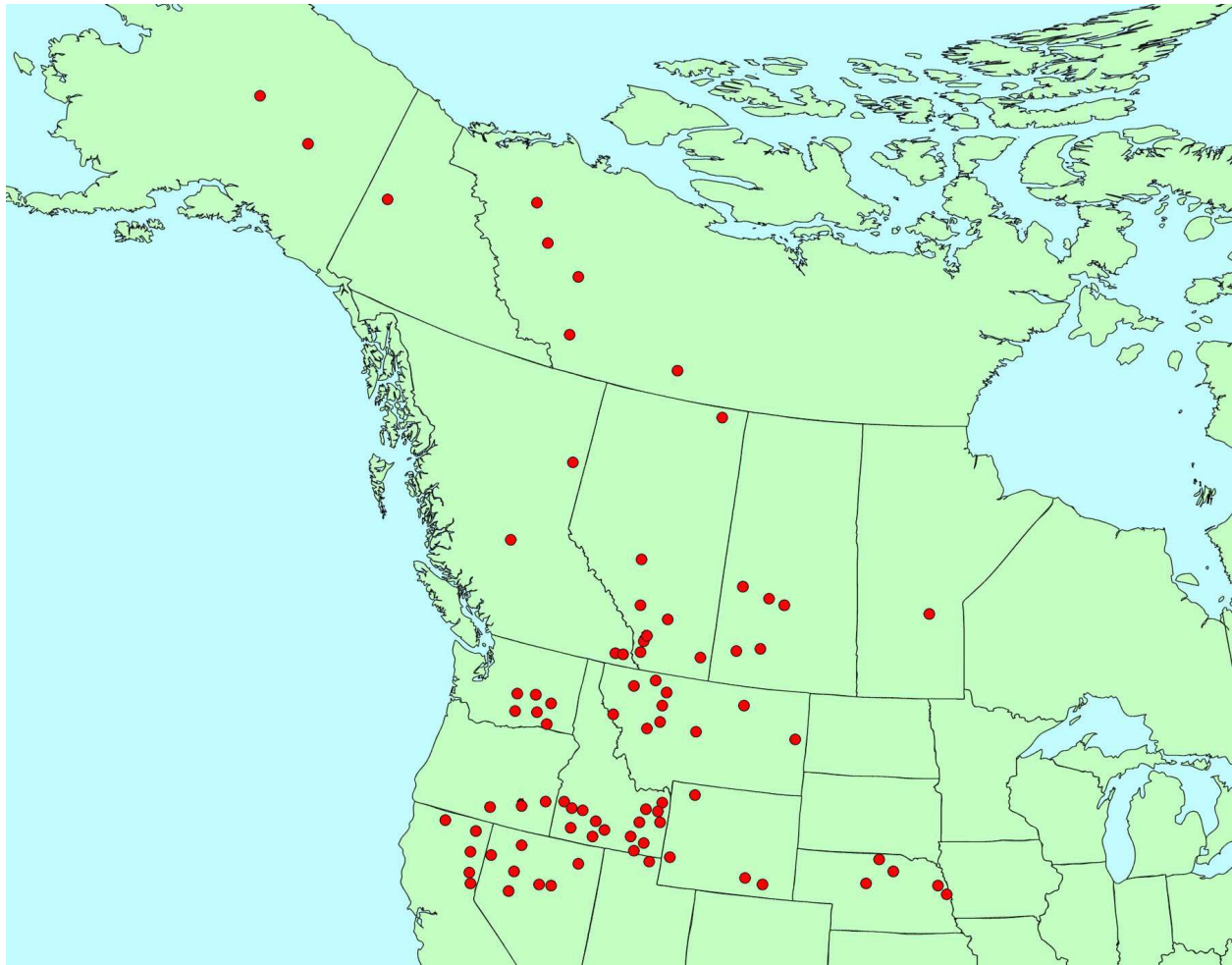


Figure 6. Distribution map of *C. verrucosa* based on material examined in connection with this study. Within the United States, each dot denotes a county record and may be representative of multiple sites within the county.

Junction, 29-V-1976, M. L. Siri & R. B. Kimsey (5, UCDC); Hallelujah Junction, 29-VI-1976, C. M. Bortfeld (2, UCDC); Hallelujah Junction, 29-VI-1976, R. M. Giblin (1, UCDC); Hallelujah Junction, 29-VI-1976, J. R. Nixon (1, UCDC); Hallelujah Junction, 29-VI-1976, D. A. Poirier (2, UCDC); Hallelujah Junction, 29-VI-1976, M. A. Rabel (1, UCDC); Hallelujah Junction, 29-VI-1976, N. J. Smith (3, UCDC); Hallelujah Junction, 29-VI-1976, P. F. Smith (1, UCDC); Hallelujah Junction, 29-VI-1976, G. M. Streett (3, UCDC); Hallelujah Junction, 5-VII-1978, S. L. Heydon (1, UCDC); Hallelujah Junction, 12-VII-1980, J. A. Skinner (1, UCDC); 2 mi. W Hallelujah Junction, 7-VI-1968, S. M. Hogue & R. L. Penrose, *Salix* (23, WFBM); Long Valley Creek, 1 km W Hallelujah Junction, elev.1509 m, 1-VIII-1974, E. L. Smith (56, CASC). Modoc Co.: South Fork District, Modoc National Forest, 1-IX-1959, J. A. Litsinger (5, EMEC). Plumas Co.: Beckwourth Pass, 14-IX-1969, F. G. Andrews, *Salix* (3, CDAE). Sierra Co.: Independence Lake, 1-VII-1976, N. Smith (4, UCDC). Siskiyou Co.: Cedarville, 15-V-1946, F. Sciaroni, prune tree (1, CDAE). **IDAHO:** [no specific locality] (1, INHS). Ada Co.: Boise, 24-VIII-1976, R. Smith (1, CIDA); Boise, elev. 2739 ft., 3-VI-1921, C. Wakeland (2, WFBM); 1.7 mi. NW Swan Falls, 21-III-1983, D. Ward, under rocks (1, CIDA). Bannock Co.: [no specific locality], 22-IX-1970, R. Jeppson (1, BYUC). Bingham Co.: Aberdeen, 7-VI-1963, K. Bishop (2, WFBM); Aberdeen, 13-VI-1963, B. Owens, on willow (1, WFBM); Aberdeen, Exp. Station, 31-VIII-1966, Q. Carpenter (1, WFBM); Fort Hall, elev. 4490 ft., 30-VI-1931, V. E. Jones (2, BYUC). Bonneville Co.: Idaho Falls, 26-VIII-1951, R. Schuster (33, EMEC); Idaho Falls, 22-VI-1957, R. A. Mackie (22, WFBM). Canyon Co.: Caldwell, 7-V-1922, D. B. Whelan (1, WFBM). Elmore Co.: Glenns Ferry, 22-V-1970, H. M. Edwards (6, WFBM). Fremont Co.: Ashton, 8-IX-1967, M. Marquis (3, CASC); Island Park, 1-VII-1978, G. A. Shook (5, CIDA); St. Anthony, 18-IX-1961, R. B. Pitman (1,

WFBM). Gooding Co.: Gooding, 25-VII-1959, W. F. Chamberlain (1, TAMU). Jefferson Co.: Rigby, elev. 4949 ft., VI-1952, H. C. Manis, *Salix* (30, WFBM). Jerome Co.: Eden, 19-VIII-1938, G. F. Knowlton, F. C. Harmston (2, EMUS); Eden, 21-VIII-1938, G. F. Knowlton, F. C. Harmston (4, EMUS); Hazelton, 7-VIII-1938, J. W. Zukel (1, WFBM). Madison Co.: Sugar, 1-X-1953, G. E. Patterson (1, EMUS). Oneida Co.: Curlew Valley Reservoir, 1-IX-1970, G. F. Knowlton (1, EMUS); Curlew Valley Reservoir, 6-VII-1972, G. F. Knowlton (1, EMUS); Holbrook, 5-VIII-1969, G. F. Knowlton (2, EMUS); 4 mi. NW Holbrook, 16-V-1969, G. F. Knowlton, G. E. Bohart (2, EMUS); Rock Creek, 22-VI-1971, G. F. Knowlton (1, EMUS). Owyhee Co.: Bruneau Sand Dunes, 15-VII-1930 (1, UCDC); Bruneau Sand Dunes, 15-IV-1961, M. M. Furniss, *Salix* (3, WFBM); Bruneau Sand Dunes, 4-V-1974, G. A. Shook (9, CIDA; 2, WFBM); Bruneau Sand Dunes, 6-V-1974, G. A. Shook (1, CIDA); Bruneau Sand Dunes, 8-III-1975, G. A. Shook (1, WFBM); Bruneau Sand Dunes, 6-IV-1975, G. A. Shook (3, WFBM); Bruneau Sand Dunes, 10-V-1975, W. H. Clark, *Salix* (4, WFBM); Bruneau Sand Dunes, 10-V-1975, W. H. & M. H. Clark (27, CIDA); Bruneau Sand Dunes, 10-V-1975, G. A. Shook (2, WFBM); Bruneau Sand Dunes, 15-V-1976, W. H. & M. H. Clark (20, CIDA); Bruneau Sand Dunes, T6S R6E Sect. 13, 15-V-1976, R. C. Biggam (45, WFBM); Duck Valley Indian Reservation, near Mountain View Reservoir, 24-V-2003, H. L. Leavitt (6, BYUC); Snake River at Rt. 45, S of Melba, 7-VII-1978, Littlefield (1, WFBM); Strike Reservoir, 12-V-1979, C. R. Baird, willow (7, CIDA). Power Co.: American Falls, 6-V-1950, E. H. Kardos, willow (2, EMUS); American Falls, 7-V-1950, G. P. Taylor (7, EMUS); American Falls, elev. 4330 ft., 28-VII-1921, C. Wakeland (2, WFBM); [no specific locality] (9, WFBM). Twin Falls Co.: Twin Falls, IX-1919 (5, CASC); Twin Falls, elev. 3700 ft., VII-1918, R. H. Smith (3, WFBM). **ILLINOIS:** [no specific locality] (1, MLUH; locality doubtful, see Comments section below). **MISSOURI:** [no specific locality] (1, INHS, locality doubtful, see Comments section below). **MONTANA:** [no specific locality] (1, INHS). Dawson Co.: [no specific locality], 12-VII-1931 (2, MTEC). Flathead Co.: Kalispell, 13-I, Wickham (1, MTEC); Kalispell, (26, INHS); Kalispell, 13-20-VI, Wickham (9, CASC); Mont. Exp. Sta., 1-VII-1926 (1, MTEC). Gallatin Co.: [no specific locality], 17-V-1955 (1, MTEC); [no specific locality], 29-V-1982 (1, MTEC); [no specific locality], 3-VI-1982 (1, MTEC). Glacier Co.: Cutbank Creek, 22-VIII-1954, P. S. Bartholomew (71, CASC). Judith Basin Co.: Ackley Lake, 29-VIII-1990, D. L. Gustafson (1, MTEC). Lewis & Clark Co.: Sun River Game Range, NW of Augusta, 24-VI-1988, C. E. Seibert (4, BYUC; 11, MTEC). Mineral Co.: Superior, 27-IV-1946, L. A. Weitz (12, CASC). Missoula Co.: Clark Fork River, 29-V-1988, S. J. Harvey, *Salix exigua* (5, BYUC; 18, MTEC); Missoula, 11-V-1958, J. Turcotley (1, MTEC). Phillips Co.: 17 mi. W Malta, West Alkali Creek, 12-VI-1989, J. Lacey, *Salix* (3, MTEC). Pondera Co.: Lake Frances, 10-VII-1991, D. L. Gustafson (1, MTEC). Powell Co.: 6 mi. E Garrison, Hwy. 12, 30-VIII-1988, S. M. Clark (1, MTEC); 6 mi. E Garrison, Hwy. 12, 30-VIII-1988, S. M. Clark, *Salix* sp. (1, BYUC). Teton Co.: Choteau, 27-V-1979, K. Shaw (1, MTEC); 15 mi. N Choteau, Eureka Lake, 21-VI-1954, R. C. Froeschner (37, MTEC); Muddy Creek, Hwy. 220, 27-VIII-1988, C. E. Seibert (2, MTEC). **NEBRASKA:** Cuming Co.: West Point, V-1987 (1, UNSM). Holt Co.: Spencer Dam, 15-21-VI-1974 (1, UNSM). Keya Paha Co.: Springview Bridge, 18-VI-1902, W. D. Pierce, ground (1, UNSM). Thomas Co.: Halsey, VII-1969 (1, UNSM). Washington Co.: Blair, 13-VII-1930, T. Mulhall, willow (7, UNSM). **NEVADA:** Elko Co.: Elburz, 27-VII-1998, C. F. Peterson (8, BYUC); Humboldt River, Hwy. 229, at Halleck, 27-VII-1998, J. G. Ritz (2, BYUC); Humboldt River, near Elburz, 27-VII-1998, B. G. Parry (4, BYUC); North Fork Humboldt River, 27-VII-1998, E. S. Atkinson (3, BYUC); North Fork Humboldt River, Devils Gate, 41°11' N 115°30' W, 30-IV-2003, R. W. Baumann & K. T. Huntzinger (1, BYUC); North Fork Humboldt River, at Elburz, 27-VII-1998, K. Cedergreen (8, BYUC); North Fork Humboldt River, at Elburz, 27-VII-1998, J. A. Robertson (33, BYUC); North Fork Humboldt River, near Elburz, 27-VII-1998, R. W. Baumann & R. G. Call (11, BYUC); North Fork Humboldt River, near Elburz, 27-VII-1998, A. Holgerson (3, BYUC); Oasis, 10-VIII-1973, T. Griswold (1, CASC). Eureka Co.: Humboldt River, Dunphy, 7-VI-2000, R. W. & C. W. Baumann (2, BYUC); Humboldt River, Dunphy, 23-VI-2001, Baumann & Ozment (16, BYUC); Humboldt River, Dunphy, 28-IV-2003, Baumann & Huntzinger (1, BYUC); Marys Creek, near Carlin, 31-III-1992, Baumann & Brooks (1, BYUC). Humboldt Co.: 4 mi. NE Golconda, 22-VI-1966, W. Gagne & J. Haddock (3, EMEC); Valmy, 13-IX-1956, T. R. Haig (1, UCDC); Winnemucca, 24-VI-1965, G. F. Knowlton (4, EMUS); Winnemucca, 16-V-1974, C. Tierman, *Salix* sp. (68, BYUC); 5 mi. N Winnemucca, 9-IX-1959, T. R. Haig (3, CDAE). Lander Co.: Humboldt River at Argenta, 12-IV-2005, B. C. Kondratieff & R. W. Baumann (16, CSUC); Humboldt River at Argenta, 40°41' N 116°44' W, 12-IV-2005, R. W. Baumann & B. C. Kondratieff (7, BYUC); Humboldt River at Argenta, elev. 4530 ft, 40.676°N 116.730°W, 21-IV-2004, S. M. Clark, *Salix exigua* (5, BYUC). Pershing Co.: Rye

Patch Reservoir, 9-VIII-1973, T. Griswold (12, CASC); Rye Patch Reservoir, 11-VI-1980, S. M. Clark (4, BYUC). Washoe Co.: Mt. Rose, 7-VII-1972, C. Goodpasture (1, UCDC); Reno, 23-VII-1940, LaR. (1, EMEC); Reno, 17-VI-1957, F. D. Parker (2, UCDC); Reno, 18-VI-1957, F. D. Parker (1, UCDC); Reno, 28-VI-1957, F. D. Parker (1, UCDC). **OREGON:** Harney Co.: Blitzen Valley, V-1936, F. Lawrence (4, UCDC); Malheur, 20-V-1977, H. H. (1, CASC); Malheur Refuge, Buena Vista, 7-V-1976, N. Cobb (1, CASC); Malheur Wildlife Refuge, elev. 4100 ft., 12-VIII-1976, J. Snively, willow (2, CASC); [no specific locality], 8-V-1976, E. H. Grubler (2, CASC). Lake Co.: Chewaucan River near Valley Falls, 16-VIII-1939, K. Gray & J. Schuh (4, TAMU); Ebert Lake, 23-VI-1933 (1, UCDC); Valley Falls, 16-VIII-1939, Schuh & Scott, *Salix* (2, EGRC). UTAH: Cache Co.: Logan Canyon, 12-IV-1960, D. Martinsen (1, EMUS); Logan Canyon, 12-V-1960, D. Martinsen (1, EMUS). **WASHINGTON:** Franklin Co.: Pasco, 12-V-1958, P. L. Sheldon (1, CASC). Grant Co.: George, 6-VI-1991, R. L. Chauvin, willow (4, EMUS); 8 mi. W George, Columbia River, 12-V-1979, B. Vogel (1, MTEC); 8 mi. W George, Columbia River, 26-IV-1980, B. Vogel (6, MTEC). Kittitas Co.: Ginkgo State Park, 14-V-1948, E. S. Ross (16, CASC); Vantage, 2-V-1947, D. W. Boddy (7, CASC); Vantage, 8-V-1949, Nelson, willow (3, FSCA); Vantage, 22-V-1954, D. W. Boddy (2, CASC); 1 mi. S Vantage, 8-V-1949, F. Ritz (7, EGRC). Walla Walla Co.: Lowden, 28-VIII-1948, G. H. Nelson (1, CDAE); Walla Walla, 14-VIII-1935, E. W. Jones (1, WFBM); Walla Walla, 9-V-1945, G. H. Nelson (2, WFBM); Walla Walla, 16-VI-1946, E. W. Jones (5, WFBM); Wallula Jct., 16-IV-1966, D. S. Horning (1, WFBM); [no specific locality] (1, WFBM). Yakima Co.: Satus, 21-VII-1924, K. E. Gibson (2, WFBM); Satus, 17-IV-1926, K. E. Gibson (13, WFBM); Satus, 7-V-1926, K. E. Gibson (10, WFBM); Satus, 21-VII-1927, K. E. Gibson (17, WFBM). **WYOMING:** [no specific locality] (1, INHS). Albany Co.: Laramie, 19-V-1994, Buffum (2, ESUW); Laramie, 20-V-1994, Buffum (10, ESUW); Laramie, 7.5 mi. NW Little Laramie River, 3-VII-1984, W. Suter (1, BYUC). Carbon Co.: Como, elev. 8000 ft. (1, EMEC). Lincoln Co.: Kemmerer, 23-VIII-1939, W. F. Chamberlain (1, TAMU). Park Co.: 2.7 mi. S Powell, 21-V-1982, R. Lavigne (2, ESUW).

NORTH AMERICA. [no specific locality] (1, MLUH, see Comments section below).

Distribution. Riley et al. (2003) listed *C. verrucosa* from Alberta, British Columbia, Manitoba, Northwest Territories, Ontario, Saskatchewan, California, Idaho, Montana, Nebraska, Nevada, Oregon, Utah, Washington, and Wyoming. Gómez-Zurita (2005) listed this species from all of these areas, as well as from Alaska. We have seen specimens also from the Yukon Territory. In connection with the present study, we have studied specimens from the sites listed in the Material Examined section above and indicated in the map (Fig. 6).

Hosts. This species has been recorded from *Salix* (Salicaceae), with *S. exigua* Nuttall specifically being mentioned (Clark et al. 2004). In the present study, we confirm this association, having personally collected the insects, both larvae and adults, from *S. exigua* and having reared them in the laboratory on this plant. Among the material we have examined, there are specimens labeled from willow, *Salix* sp., *S. alaxensis* (Andersson) Coville, *S. exigua*, and *S. interior* Rowlee [= *S. exigua*]. We believe that the occurrence of a single specimen on a prune tree [*Prunus* sp., Rosaceae] was incidental.

Comments. The original description of *C. verrucosa* is rather short and uninformative (Suffrian 1858). Although it best matches beetles regarded as this species by Schaeffer (1934) and subsequent authors, the type specimen could possibly be an unusually marked specimen of *C. multipunctata* or even some other species. In the original publication, Suffrian stated that the description was based on material from the Sturm collection. This collection is now housed at the Zoologische Staatssammlung in Munich, Germany. However, curator Martin Baehr (personal communication) was unable to find type material of *C. verrucosa* in that museum. Much of the Suffrian collection is now preserved at the Martin-Luther-Universität in Halle, Germany, and it includes two specimens identified as *C. verrucosa* (Karla Schneider, personal communication). We were able to borrow and photograph both of these specimens, and they are indeed the same species that is normally regarded as *C. verrucosa* (Fig. 5). The specimens are labeled with code numbers only, but curator Karla Schneider (personal communication) stated that specimen 31733 is from "Illionis" [sic] and specimen 27673 is from "Nordamerika."

The type locality given by Suffrian (1858) is Missouri, and a single specimen from the Illinois Natural History Survey is labeled "Mo." However, the actual occurrence of this more western species in Missouri is extremely doubtful. In their detailed treatment of the Chrysomelidae of Missouri, Riley and Enns (1979,

1982) did not report seeing any specimens. Most likely, the type material was collected even earlier than the original description in 1858, during an era when the definition of Missouri may have been very broad. Perhaps, the type locality indicates only that the type material was collected somewhere in the Missouri River drainage, which extends far beyond the present-day limits of the state of Missouri. It is interesting that Say's (1824) "Var. a" of *Chrysomela multipunctata* Say was probably based on specimens of *C. verrucosa*, with the collection locality also being reported as "Missouri." The Illinois specimen mentioned in the preceding paragraph may similarly have come from beyond the present-day limits of the state with that name. In our distribution map, we have not included sites for either Missouri or Illinois.

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